# REPORT

R. Berkelmans · B. L. Willis

# Seasonal and local spatial patterns in the upper thermal limits of corals on the inshore Central Great Barrier Reef

**Abstract** Experimental studies of the upper thermal limits of corals from Orpheus Island, an inshore reef in the central Great Barrier Reef, show that *Acropora formosa* has a 5-day 50%-bleaching threshold of between 31 and 32 °C in summer, only 2 to 3 °C higher than local mean summer temperatures (29 °C). Summer bleaching thresholds for *Pocillopora damicornis* and *A. elseyi* were 1 °C higher (between 32 and 33 °C). The winter bleaching threshold of *Pocillopora damicornis* was 1 °C lower than its summer threshold, indicating that seasonal acclimatisation may take place. This seasonal difference raises the possibility that at least some corals may be capable of short-term thermal acclimatisation. Neither *P. damicornis* nor *A. elseyi* showed habitat-specific (reef flat versus reef slope) differences in bleaching thresholds. Further, colonies of *P. damicornis* collected from sites 3 km apart also showed no difference in bleaching threshold despite populations of this species responding differently at these two sites during a natural bleaching event. The bleaching thresholds determined in this study are best considered as the maximum tolerable temperatures for local populations of these species because they were determined in the absence of additional stressors (e.g. high light) which often co-occur during natural bleaching events. We consider the 5-day 50% bleaching thresholds determined in these experiments to be fair indicators of upper thermal limits, because > 50% of a sample population died when allowed to recover in situ. We found a delay of up to a month in the bleaching response of corals following thermal stress, a result that has implications for identifying the timing of stressful conditions in natural bleaching events.

# Introduction

Although coral bleaching events have been observed as far back as the 1870s, there has been a dramatic increase in the number of reported incidents of mass coral bleaching in the scientific literature since the 1980s (Glynn 1993; Brown 1997). This apparent trend has led to worldwide concern regarding the current health of coral reefs and status of economies dependent on them (Meehan and Ostrander 1997). Bleaching is a stress response that is manifested as the dissociation of the coral-algal symbiosis, causing corals to appear pale or white (Yonge and Nicholls 1931). Elevated temperatures, of as little as 1–2 °C above mean monthly summer values, are a major cause of bleaching (Glynn et al. 1988; Drollet et al. 1994).

To gain insights into the degree to which temperature anomalies are capable of structuring coral assemblages, we need to quantify upper thermal tolerances for a range of coral species. Results for the few species whose thermal tolerances have been investigated experimentally concur with data collected during natural bleaching events and confirm that corals live close to their upper thermal limits (Jokiel and Coles 1990; Glynn and D'Croz 1990). Experimental studies also indicate that there is considerable variation in thermal tolerance between species (Edmundson 1928; Coles et al. 1976) and between populations from widely separated geographic regions (Coles et al. 1976; Marcus and Thoraug 1981; Glynn et al. 1988). These studies may explain, in part, variation in the intensity of bleaching between species in localised events and between

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geographically disparate populations of the same species in widespread bleaching events.

Less well understood is the common observation that bleaching is frequently patchy within species on localised scales. For example, several studies have documented or claimed a higher proportion of corals bleaching on the reef slope compared with the reef flat (Hoeksema 1991), on outer rim reefs compared to inner lagoonal sites (Cook et al. 1990) and on the fore reef compared with the back reef (Goreau 1990). One of the suggested reasons for differential bleaching between habitats is that corals exposed to variable temperatures, such as those on the reef flat or lagoon, are better acclimatised to thermal stress than those experiencing less variable conditions, such as reef-slope or rim-reef corals (Cook et al. 1990; Hoeksema 1991). There are also reports of considerable variation in bleaching over small spatial scales within the same habitat (Oliver 1985) and in the proportion of corals bleached between sites separated by only a few kilometres. Hoegh-Guldberg and Salvat (1995) found a mean of 72% of corals bleached on the NE side of Moorea, French Polynesia, but fewer corals (mean = 40%) bleached on the NW side less than 10 km away. Genetic variation between coral populations and/or variable thermal tolerance limits of different zooxanthellae strains may contribute to such variation in bleaching on local scales (see Buddemeier and Fautin 1993; Knowlton and Jackson 1994; Rowan and Knowlton 1995). Differential acclimatisation of corals between sites due to differences in thermal history may also occur but is largely unexplored. To better understand the role of temperature anomalies in structuring coral assemblages at a local scale, knowledge of variability in upper thermal limits over small spatial and temporal scales is needed.

Bleaching has been used to detect upper thermal limits of corals in a number of studies (e.g. Coles et al. 1976; Jokiel and Coles 1977; Coles and Jokiel 1978; Marcus and Thoraug 1981; Glynn and D'Croz 1990). However, the appropriateness of the bleaching response as an indicator of tolerance limits is not clear. Upper thermal limits of organisms are traditionally defined as the temperature at which 50% of the sample population dies after a specified period of exposure, often expressed as the $T_{L50}$ (Schmidt-Nielson 1990). Using coral bleaching as an indicator of upper thermal limit is convenient because it avoids the necessity to monitor the recovery of corals or their decline to death following a predetermined period of thermal stress. However, because corals may recover following bleaching (Gleason 1993; Drollet et al. 1994), it is not clear how to relate a bleaching threshold temperature to an upper thermal limit.

In this study we determine the upper thermal limits for three coral species and evaluate the usefulness of bleaching thresholds as indicators of traditional $T_{L50}$. We also investigate whether upper thermal limits vary seasonally or over small spatial scales to better understand the role of localised temperature anomalies in structuring coral assemblages. Specifically, we investigate whether temperature tolerances vary between winter and summer, between corals collected from the reef slope and reef flat and between colonies from equivalent habitats at sites 3 km apart.

## Materials and methods

We investigated upper thermal tolerances of three coral species, *Acropora formosa* (Dana 1846), *Acropora elseyi* (Brook 1892) and *Pocillopora damicornis* (Linneus 1758) from fringing reefs adjacent to Orpheus Island Research Station (latitude 18.34°S, longitude 146.29°E), located on the Great Barrier Reef near Townsville, Australia. These species were chosen because they are often reported as being among the first to show bleaching symptoms during natural bleaching events (Oliver 1985) and because of their high abundance on many Indo-Pacific reefs.

### Experimental protocols

Experiments were conducted at Orpheus Island Research Station in round fibreglass tanks, each 2.4 m in diameter, filled with approximately 1500 l of seawater and fitted with a 3 KW electric heating element. Filtered seawater from the upper reef slope in Pioneer Bay at Orpheus Island ( ∼ 3 m depth) was pumped continuously into each tank at a rate of 4 l·min⁻¹, which exchanged the water on average every 6 h. Submersible pumps ensured that water within each tank was well mixed. Experimental temperatures in each tank were monitored at 10-min intervals using data loggers throughout each experimental period and on an ongoing basis in an adjacent bay (Cattle Bay) at 30-min intervals. Data loggers were calibrated using a digital NATA certified thermometer, and are accurate to ± 0.2 °C. Control of temperature in the heated tanks was either automatic via a computerised process control system or manual by measuring and adjusting temperatures every 15 min. Spot checks at different places within the tanks confirmed that spatial variation in temperature within each tank was generally less than 0.1 °C. Temperatures of the treatments and control are presented in Fig. 1. Tanks were covered with 70% shade cloth (30% transmitted light) to avoid any potentially confounding effects of high light intensity on the thermal tolerance of corals. The levels of transmitted light (ranging from approximately 400 to 550 µE·m⁻²·s⁻¹ between experiments) are equivalent to those experienced by corals at approximately 5 m depth at mean tide level (Berkelmans unpublished data). Although ambient light was reduced to a level where it was unlikely to have influenced the bleaching response of corals in individual experiments, seasonal variation in light intensity might alter bleaching responses between summer and winter within a species. To compare light levels among experiments, sea surface light (photosynthetically active radiation) conditions were monitored at Myrmidon Reef (approximately 90 km NE of Orpheus Island). Light and temperature data at the time of the experiments are presented in Table 1. Light values are means of 5 s scans, recorded half-hourly and averaged between 10 am and 3 pm each day, representing the period of highest daily irradiance (data courtesy of Australian Institute of Marine Science).

Four tanks were used in the experiments, three for simultaneously heating experimental corals to different target temperatures and a fourth for maintaining them at ambient temperatures as a control. Temperature treatments were allocated randomly to tanks for the first experiment and deliberately rotated for later experiments to avoid potential bias from tank effects. Corals were allowed to adjust

**Fig. 1a–c** Experimental conditions during: **a** first summer experiment (effects of species and summer temperatures on upper thermal limits); **b** second summer experiment (effects of species and habitat on summer upper thermal limits); and **c** winter experiment (effects of site and season on winter upper thermal limits, bleaching as an indicator of upper thermal limits). Box plots show median, 50th quartile and the total range in temperature. Adjoining tables show means and standard deviations
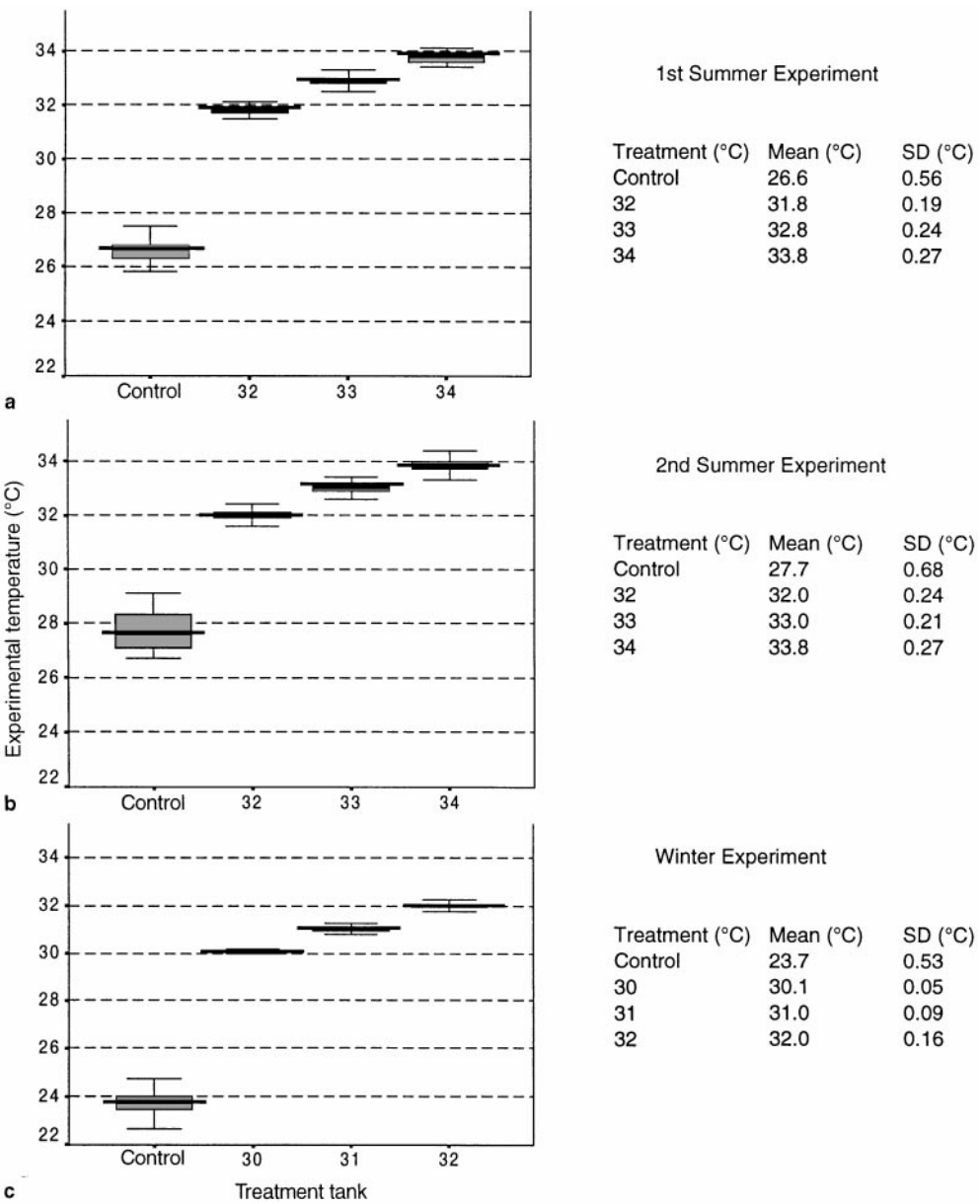


1st Summer Experiment

| Treatment (°C) | Mean (°C) | SD (°C) |
|---|---|---|
| Control | 26.6 | 0.56 |
| 32 | 31.8 | 0.19 |
| 33 | 32.8 | 0.24 |
| 34 | 33.8 | 0.27 |

2nd Summer Experiment

| Treatment (°C) | Mean (°C) | SD (°C) |
|---|---|---|
| Control | 27.7 | 0.68 |
| 32 | 32.0 | 0.24 |
| 33 | 33.0 | 0.21 |
| 34 | 33.8 | 0.27 |

Winter Experiment

| Treatment (°C) | Mean (°C) | SD (°C) |
|---|---|---|
| Control | 23.7 | 0.53 |
| 30 | 30.1 | 0.05 |
| 31 | 31.0 | 0.09 |
| 32 | 32.0 | 0.16 |

**Table 1** Ambient sea temperature and surface light levels before, during and after temperature experiments. Temperatures (°C $\pm$ SD) measured by in situ data loggers recording at 30 min intervals at Cattle Bay, Orpheus Island. Light ($\mu E.m^{-2}.s^{-1} \pm$ SD) measured as photosynthetically active radiation (PAR) at Myrmidon Reef (approximately 90 km NE of Orpheus Island)

| | Ambient conditions | | | | | |
|---|---|---|---|---|---|---|
| | 14 days before experiment | | During experiment | | 0–34 days after experiment | |
| | PAR | Temperature | PAR | Temperature | PAR | Temperature |
| 1st summer | 1271 $\pm$ 430 | Not available | 1229 $\pm$ 566 | 28.4 $\pm$ 0.25 | Not applicable | Not applicable |
| 2nd summer | 2002 $\pm$ 114 | 28.9 $\pm$ 0.24 | 1864 $\pm$ 133 | 28.2 $\pm$ 0.14 | Not applicable | Not applicable |
| Winter | 1397 $\pm$ 244 | 22.9 $\pm$ 0.12 | 1513 $\pm$ 59 | 23.1 $\pm$ 0.11 | 1569 $\pm$ 275 | 23.4 $\pm$ 0.44 |

to tank conditions for two days prior to commencement of temperature experiments. Treatment tanks were heated slowly ( $< 0.5$ °C/h) to the target temperatures and maintained there for five days. This rate of temperature rise is less than that experienced by local reef flat corals during spring tides when temperatures commonly vary by more than 1 °C/h, (Berkelmans and Oliver in preparation). Temperature experiments were conducted on three occasions: two in summer/autumn (15 – 20 February 1993: effects of species and summer

bleaching threshold; and 4 – 9 April 1993: effects of species and habitat on bleaching threshold) and one in winter (10 – 15 August 1993: effects of site and winter bleaching threshold).

### Bleaching thresholds

We used a visual estimate of the degree of bleaching as the variable for measuring the response of corals to experimental temperature manipulations. Corals were allocated to one of three categories based on appearance: 'normal' i.e. no visible loss of colour; 'moderate bleaching' i.e. corals pale, but still with a significant amount of colour; and 'heavy bleaching' i.e. corals mostly white or dead. Upper thermal limits were defined as the temperature at which 50% or more of corals were moderately or heavily bleached at the end of the 5-day exposure period.

Zooxanthellae densities were measured in samples from each response category for two of our study species, *Pocillopora damicornis* and *Acropora formosa*, to determine the approximate relationship between tissue colour and zooxanthellae density under our experimental conditions. Zooxanthellae densities were determined from branch tips (*P. damicornis*: 2.5–3.0 cm in length and *A. formosa*: 4.5–6.0 cm in length) subsampled from four experimental colonies per response category. Tissues were removed using a Water-Pik into 100 ml of seawater and homogenised with a blender for 1 min. Eight replicate zooxanthellae counts per branch sample were made using a haemocytometer.

### Summer upper thermal limits and the effect of species

To determine summer upper thermal limits for three coral species and establish whether they differ, we subjected 20 fragments (15–20 cm in length) of *Acropora formosa*, *A. elseyi* and *Pocillopora damicornis* to four temperature treatments (32, 33, 34 °C and an unheated control (26.6 °C $\pm$ 0.6° SD). Corals were collected from the upper reef slope between 2 and 4 m depth at mean tide level. Branches were sampled from colonies that were spaced over a distance of approximately 200 m along the narrow fringing reef in Cattle Bay (Orpheus Island). Fragments collected for all experiments included a range of morphological types and were therefore likely to have represented a range of genetic variants. Branches were allocated haphazardly to the different treatments. The 32 °C temperature treatment was close to or slightly above the range of local maxima in daily summer temperatures (GBRMPA 1999). Treatment tanks were heated slowly ( < 0.5 °C/h) to target temperatures and maintained there for five days, after which the condition of each fragment was visually assessed. Chi-squared analysis was used to compare the proportions of bleached corals between species in each temperature treatment (2 × 4 contingency tables).

### Effect of tanks and habitat of origin on upper thermal limits

To determine if tank effects were confounding our determinations of upper thermal limits, we repeated the summer temperature experiments during a similar ambient temperature regime (Table 1) assigning temperature treatments to different tanks. To simultaneously establish if conspecifics collected from different habitats have different upper thermal limits, we collected fragments of each of *Pocillopora damicornis* and *Acropora elseyi* from both the reef flat and reef slope in April 1993. Reef flat corals normally experience a highly variable temperature regime (up to 8 °C over 6 h) whereas diurnal variation is typically less than 1 °C/day for reef slope corals (Berkelmans and Oliver in preparation). Thirty fragments (10–15 cm in length) from each habitat for each species were randomly allocated to one of four temperature treatments (32, 33, 34 °C and an ambient control (27.7 °C $\pm$ 0.7 °SD), $n = 15$ fragments per temperature treat-

ment per habitat). To maximise our chances of detecting differences in tolerance limits in corals from different habitats, corals from the reef flat were collected from the shallowest zone in which they occur ( ~ mean low water springs) and those from the reef slope from the deepest zone in which they occur ( ~ 6 m). The duration of the treatments was again five days with corals being heated slowly to their respective target temperatures ( < 0.5 °C/h).

### Winter upper thermal limits and the effect of site of origin

To determine whether upper thermal limits of *Pocillopora damicornis* differed among seasons or among colonies from different sites, we conducted a similar temperature experiment in August 1993 (austral winter) using corals collected from two adjacent reefs. Fragments (10–15 cm in length) were collected from fringing reefs at Orpheus Island and adjacent Pelorus Island at a depth of approximately 3 m at mean tide level. These sites are approximately 3 km apart and colonies at equivalent depths responded quite differently during a natural bleaching event in 1994. During this event, 80–100% of *P. damicornis* at Orpheus Island bleached, whereas less than 10% of colonies at Pelorus Island were affected (R. Berkelmans unpublished. data). Thirty fragments from each site were placed in each of four treatment temperatures (30, 31 and 32 °C and an ambient control (23.7 °C $\pm$ 0.5 °SD). Treatments all represented temperatures below bleaching thresholds found during the summer experiments (see Results). Treatment tanks were heated to target temperatures at a rate not exceeding those experienced during natural diurnal fluctuations ( < 0.5 °C/h) and maintained at those temperatures for five days, after which the condition of the corals was visually assessed. Chi-squared analysis was used to compare the proportion of bleached coral between sites and between habitats in each temperature treatment (2 × 4 contingency tables).

### Relationship between bleaching and upper thermal limit

To determine whether bleaching is a good indicator of traditional $T_{L50}$, we allowed corals from the winter experiment, including ambient 'controls', to cool to ambient temperatures ( ~ 23 °C) over 36 h (temperature change < 0.5 °C/h). Corals were then returned to a recovery site at the depth and reef of their origin. Corals were transported submerged in bins of water and then secured to wire racks in situ. Their recovery was assessed at 14 days, 34 days and 84 days after experimental heating. At each census, corals were classified according to their condition into four categories: unbleached, moderately bleached, heavily bleached and dead ( > 50% partial mortality).

## Results

### Bleaching thresholds

Zooxanthellae counts of representative samples for each of the response categories showed that our visual assessment of colour corresponded to easily discernible bleaching categories. The pale colour of moderately bleached corals corresponded on average to a 57% reduction in the density of zooxanthellae in *P. damicornis* and a 59% reduction in *A. formosa* compared to unbleached tissue (Fig. 2). Similarly, the white colour of heavily bleached corals corresponded to an 88% reduction in the density of zooxanthellae in *P. damicornis* and an 89% reduction in *A. formosa*.
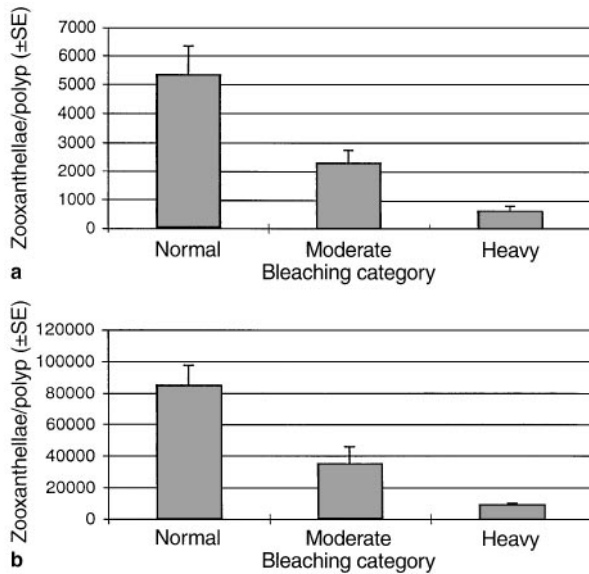
**Fig. 2a,b** Mean zooxanthellae densities ( $\pm$ SE, $n = 4$ colonies/species) in the bleaching categories recognised visually for: **a** *Pocillopora damicornis* (mean polyp density $= 60 \pm 4$ (SE) polyps.cm$^{-2}$), and **b** *Acropora formosa* (mean polyp density $= 21 \pm 2$ (SE) polyps.cm$^{-2}$)

## Summer upper thermal limits

Experimental temperature manipulations revealed a distinct bleaching threshold for the three coral species we examined. No colonies of *Pocillopora damicornis* bleached at 32 °C after experiencing five days of heating to this temperature in summer. At 33 °C, however, 60% of colonies were either moderately or heavily bleached and at 34 °C, all were either heavily bleached or dead (Fig. 3a). Daily observations of corals showed a continuing increase in the number of colonies bleaching and in the intensity of the response for the first four days. Patterns in responses throughout the time course of the experiment were clear and consistently different between temperature treatments. Twenty-four hours after reaching target temperatures, only three fragments of *P. damicornis* had commenced to pale slightly in the 33 °C treatment, whereas all 20 colonies showed evidence of bleaching in the 34 °C treatment. After 48 h, all colonies of *P. damicornis* at 33 °C were pale (moderately bleached) except for one that was white (heavily bleached), whereas all colonies at 34 °C were white. After 72 h, the loss of colour intensified in the 33 °C treatment, whereas tissue began to slough off in 11 out of 20 colonies in the 34 °C treatment. Therefore, the summer upper thermal limit for *P. damicornis*, defined as the temperature at which 50% of corals were moderately or heavily bleached after five days of thermal exposure, is between 32 °C and 33 °C.

*Acropora elseyi*'s summer bleaching threshold did not differ significantly from that of *P. damicornis* ($\chi^2 = 4.95$, $df = 3$, $P > 0.25$), but *A. formosa*'s threshold was significantly lower ($\chi^2 = 13.63$, $df = 3$, $P < 0.01$).
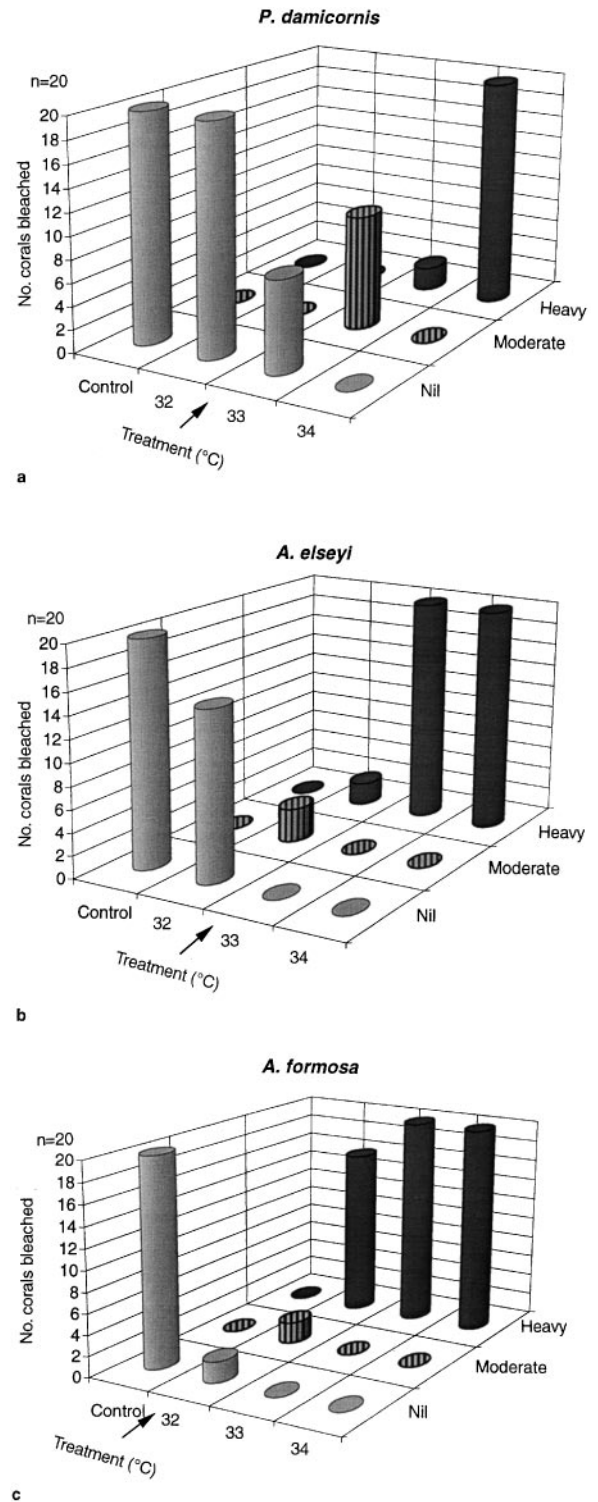






Fig. 3a–c Experimental determination of summer upper thermal limits for three coral species: **a** *Pocillopora damicornis*, **b** *Acropora elseyi* and **c** *A. formosa*. Bleaching state of corals is represented on the z-axis. Arrows approximate species-specific upper thermal limits ($n = 20$ colonies per species for each temperature treatment)

Only 25% of colonies of *A. elseyi* showed signs of bleaching after five days at 32 °C, compared to 90% for *A. formosa* (Fig. 3b, c). However, for *A. elseyi* and

*A. formosa*, all colonies were heavily bleached or dead at 33 °C (Fig. 3b, c). The summer upper thermal limit is therefore between 32 °C and 33 °C for *A. elseyi* and less than 32 °C for *A. formosa*. If *A. formosa*, like *P. damicornis* and *A. elseyi* exhibits an 'all-or-nothing response' one degree either side of its bleaching threshold, the upper thermal limit for *A. formosa* is likely to be between 31 °C and 32 °C.

The onset of bleaching in *A. formosa* was rapid in the highest temperature treatments, with 17 out of 20 colonies becoming pale after 12 h at 33 °C and 15 out of 20 colonies being white or dead at 34 °C. After 24 h, half the 33 °C colonies were white or dead, while all colonies were white or dead at 34 °C. The onset of bleaching in *A. elseyi* was intermediate, with 4 out of 20 colonies becoming pale but none white after 24 h at 33 °C, and 11 out of 20 being white and the rest pale at 34 °C.
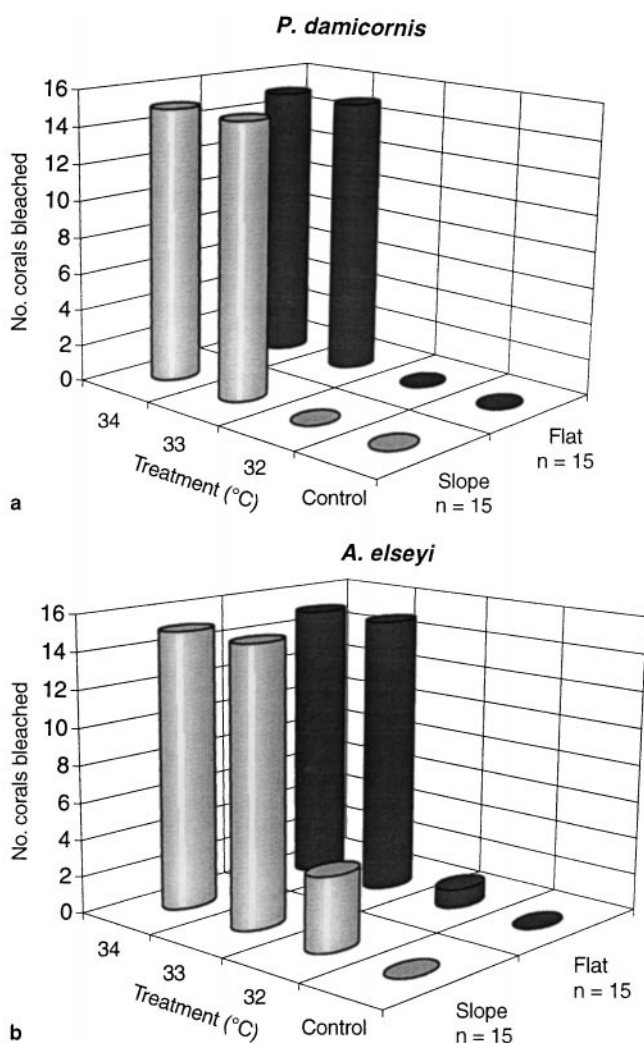


**Fig. 4a,b** Habitat comparison of summer upper thermal limits for: **a** *Pocillopora damicornis* and **b** *A. elseyi*. Reef flat corals were collected from 0 m depth (chart datum) and reef slope corals from approximately 6 m depth at mean tide. (*n* = 15 colonies per species for each temperature treatment)

A repeat of the temperature experiments in April, when ambient temperature regimes were similar (Table 1), produced similar bleaching responses. No colonies of *Pocillopora damicornis* bleached at 32 °C whereas most bleached at 33 °C, although more corals were heavily bleached in the latter treatment in the second experiment (Fig. 4a). Bleaching threshold temperatures were also identical for *A. elseyi* in the second experiment (Fig. 4b). The consistency in results between the two 'summer' experiments and the very large effect sizes observed between temperature treatments for the bleached and unbleached categories suggest that tank effects were negligible.

Effect of habitat of origin on upper thermal limits

Results of the habitat comparison showed little difference in the bleaching responses of corals collected from the reef flat and reef slope. For *Pocillopora damicornis*, neither the reef flat nor the reef slope corals bleached at 32 °C after five days of exposure, but all colonies from both habitats were moderately or heavily bleached at 33 °C (Fig. 4a). Four out of 15 colonies of *A. elseyi* collected from the reef slope were moderately or heavily bleached at 32 °C compared to one out of 15 reef flat colonies, but this difference was not significant ($\chi^2 = 1.65$, $df = 3$, $P > 0.5$) (Fig. 4b).

Seasonal variation in upper thermal limits

Temperature experiments repeated for *Pocillopora damicornis* in winter indicate that upper thermal tolerances vary between seasons. Sixty-five percent of corals were either moderately or heavily bleached after five days at 32 °C in winter (Fig. 5). In contrast, no colonies bleached at this temperature in the summer experiments following equivalent thermal exposures (Fig. 5). The winter 5-day maximum upper thermal limit for *P. damicornis* is therefore between 31 °C and 32 °C, approximately 1 °C lower than the summer threshold.

Effect of site of origin on upper thermal limits

A comparison of winter thermal tolerances between colonies of *Pocillopora damicornis* collected from Orpheus and Pelorus islands, as measured by the 5-day no-bleaching threshold, showed little difference in bleaching response between colonies from these sites. Corals from both sites showed little ( < 10%) or no bleaching at 30 °C and 31 °C, but exhibited dramatic and equivalent bleaching responses at 32 °C (Fig. 6). There was no significant difference in the winter upper thermal limits of *P. damicornis* for colonies originating from the two sites ($\chi^2 = 4.51$, $df = 3$, $P > 0.1$).
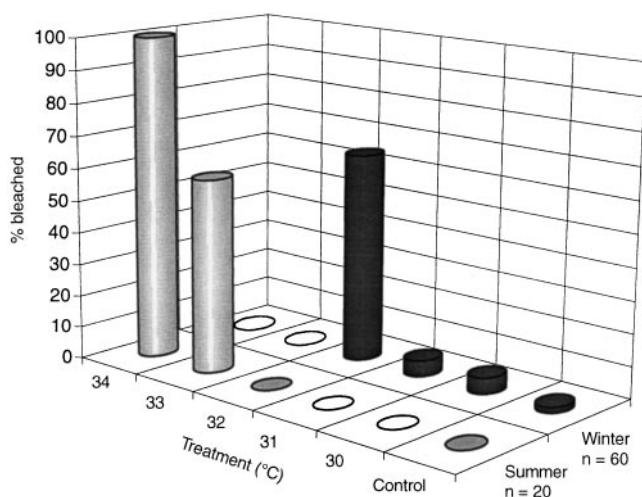
**Fig. 5** Seasonal variation in the upper thermal limits of *Pocillopora damicornis*. Histograms are totals for the moderate and heavy bleaching categories combined (*n* = 20 colonies in the summer and 60 in the winter treatment)
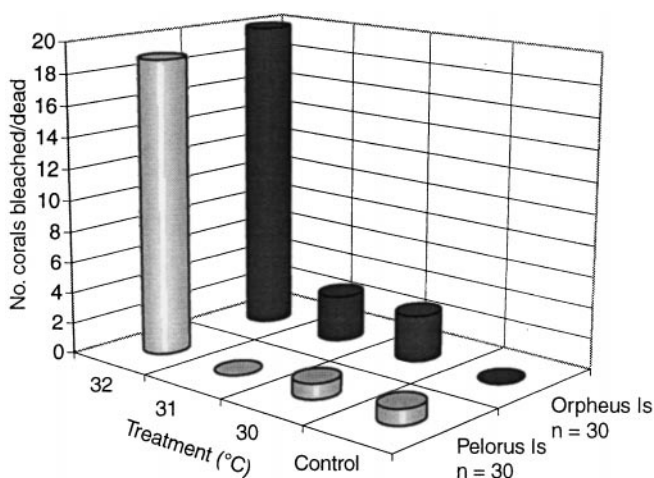


**Fig. 6** Site comparison of the bleaching response of *Pocillopora damicornis* during winter from reefs approximately 3 km apart at Orpheus and Pelorus islands (*n* = 30 colonies per temperature treatment)

Relationship between bleaching and upper thermal limit

The recovery of *Pocillopora damicornis* colonies returned to their site of origin following the winter bleaching experiment correlated with the post-experiment bleaching state of colonies. We found that the initial number of heavily bleached corals approximately predicted the number that died within one month (Fig. 7). This was despite the fact that there was a substantial delay in the bleaching response of corals from the warmest temperature treatment (32 °C). In the first 14 days after experimental warming, the number of unbleached corals decreased by 17%, while the number

of heavily bleached corals increased by 8% (Fig. 7b). Overall, nearly half of the corals deteriorated in condition during the first 14 days of being returned to the field, while only two recovered. Over the next 20 days, the number of dead corals increased by 22%. Between 14 and 34 days after the experiment, more than half of the colonies continued to deteriorate, while only six (11%) improved in condition. Light levels are unlikely to have been a factor in bringing on this delayed bleaching response as average light levels during the first 34 days of recovery were very similar to those experienced during the temperature experiment (Table 1). Eighty-four days after thermal treatment, the condition of the corals appeared to have stabilised: corals had either recovered or died, except for one colony that remained pale. All of the heavily bleached corals and approximately half of the moderately bleached corals (i.e. 51% of the total sample) died. Thus, the heavily bleached category (as scored immediately following the temperature treatment) was a good predictor of subsequent mortality in these species, but the ultimate fate of moderately bleached corals was more variable. Nevertheless, in combination, these two categories provide a rough indicator of the classic physiological determination of 'upper thermal limit' (i.e. more than 50% dead, Schmidt-Nielson 1990) under these experimental conditions. The comparatively low incidence of mortality and general lack of a delayed response only 1 °C below the winter thermal maximum of *Pocillopora damicornis* (Fig. 7a), suggests that a discrete threshold exists between tolerable and intolerable temperatures.

The approximate correlation between 'upper thermal limit' and bleaching intensity immediately following stress is further illustrated by the fate of unbleached colonies during the recovery period. Although ten out of the 53 colonies were in apparent good health at the end of the temperature experiment, their condition deteriorated 14 – 34 days later with colonies undergoing moderate or heavy bleaching. However, all these colonies made a full recovery 84 days after their return to the field. In contrast, all 15 corals that were heavily bleached at the end of the temperature experiment died.

## Discussion

Our results confirm the precarious balance between tolerable and intolerable thermal conditions that exists for some tropical corals. The upper thermal limit of Orpheus Island corals in summer, based on experimental bleaching thresholds for 5-day exposure periods, is between 32 °C and 33 °C for *Pocillopora damicornis* and *Acropora elseyi* and is likely to be between 31 °C and 32 °C for *Acropora formosa*. As these limits were determined in the absence of high levels of visible light, a potentially synergistic stress factor

**Fig. 7a,b** Delayed bleaching response of *Pocillopora damicornis* colonies returned to the field after: **a** 5 days at 31 °C (*n* = 47); and **b** 5 days at 32 °C (*n* = 53)
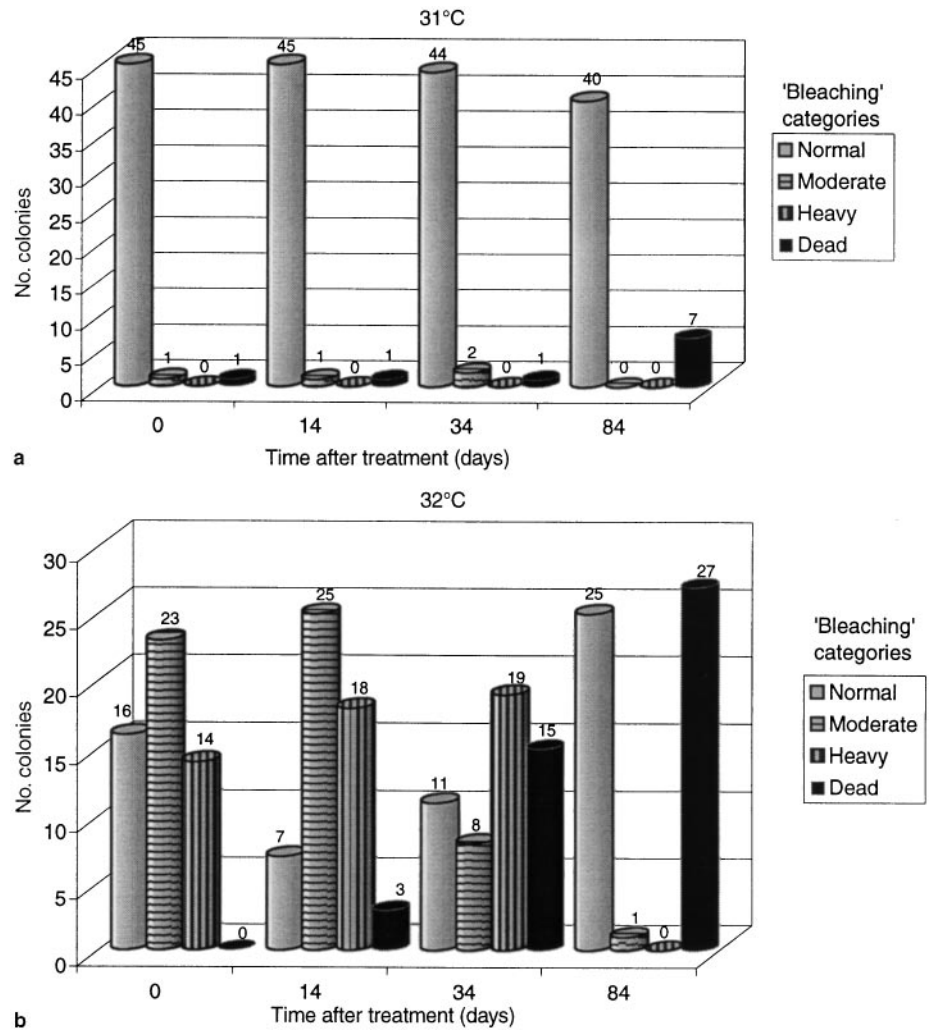


(Coles and Jokiel 1978), these figures may be close to the *maximum* upper thermal limits for these species locally and for this exposure period. Mean summer temperatures at Orpheus Island averaged 28.6 °C ± 0.9 °SD between 1993 and 1998 and temperatures periodically rise above 31 °C for short time intervals (GBRMPA 1999). Coles et al. (1976) reported a similar upper thermal limit of approximately 31 °C for two species of *Acropora* (*A. formosa* and *A. hyacinthus*) at Enewetak in the Marshall Islands, where mean summer temperatures are also approximately 29 °C (Coles et al. 1976). In contrast, the upper thermal limit we report for *P. damicornis* from Orpheus Island is approximately 2 °C higher than the limit Coles et al. (1976) reported for this species from Hawaii (mean summer temperature, 26.5 °C) for a similar exposure period, and 1 °C higher than the limit Glynn and D'Croz (1990) reported for *P. damicornis* from the Gulf of Panama for 14 days of exposure (mean summer temperature, 28 °C). These comparisons suggest local adaptations in the thermal resistance of corals that are dependent on ambient summer temperatures. Irrespective of geography, upper thermal limits of thermally sensitive corals appear to be within 2–2.5 °C of mean summer temperatures.

We found that the threshold between tolerable and intolerable thermal conditions that governs zooxanthellae expulsion is very clearly defined, illustrating the thermal sensitivity of the coral-algal symbiotic relationship. The bleaching response was triggered as an almost 'all or nothing' effect in temperature treatments only 1 °C apart. At temperatures 1 °C below the 5-day upper thermal limit, very few colonies of *Pocillopora damicornis* bleached either immediately following exposure or as a delayed response. These results are consistent with physiological data that show a sharp decline in growth of corals at temperatures only a few degrees above optimum levels. Jokiel and Coles (1977) showed that growth and calcification in *Montipora verrucosa*, *P. damicornis* and *Fungia scutaria* declined rapidly at only 2 °C above the temperature of optimal growth. Similarly, Houck et al. (1977) showed that the linear extension of *Porites lobata* decreased to zero at 28.5 °C,

which was only 1.5 °C above the temperature at which its growth peaked.

The vulnerability of corals to bleaching is likely to depend on how frequently average daily temperatures of 2–2.5 °C above mean summer values are exceeded in nature and the duration of such critical thermal exposures. Sea temperature records at Orpheus Island show that average daily temperatures (determined from half-hourly recordings) exceeded 31 °C on six days between 1993 and 1998, while daily maxima exceeded 31 °C on 76 days and 32 °C on ten days during this period. Therefore, sensitive coral species like the acroporids and pocilloporids must live either at their thermal tolerance limits for short periods of time or at a fraction of a degree below them for significant periods of time during summer. This will almost certainly make these genera highly vulnerable to any kind of additional stress during 'normal' summer conditions. At nearby Magnetic Island (75 km south of Orpheus Island), average daily reef-slope temperatures exceeded 31 °C during six out of eight summers between 1991 and 1998 and exceeded 32 °C during three summers (1992, 1994 and 1998). The number of consecutive days where average daily temperatures exceeded 31 °C ranged between 1 and 20, while the number of consecutive days exceeding 32 °C ranged between 2 and 5 (GRMPA 1999). In 1992 and 1994 these high temperature events coincided with minor coral bleaching, while in 1998 they coincided with a major bleaching event (Berkelmans and Oliver 1999).

This is the first reported experimental determination of between-season differences in upper thermal limits of corals. Our results suggest that limited natural acclimatisation to temperature may take place seasonally in some coral species. The winter maximum upper thermal limit for *Pocillopora damicornis* for a 5-day exposure is between 31 °C and 32 °C, 1 °C lower than its summer limit (Fig. 5). The reduced thermal tolerance of *P. damicornis* in winter is not explained by differences in light conditions between summer and winter. Winter light levels of $1513 \pm 59 \ \mu E.m^{-2}.s^{-1}$ were intermediate between those experienced during the two summer experiments, as were the light levels in the 14 days prior to each experiment, yet the winter bleaching threshold was lower. Furthermore light intensities between the two summer experiments were quite different at $1229 \pm 566$ and $1864 \pm 133 \ \mu E.m^{-2}.s^{-1}$ (Table 1), yet the transition temperature for beaching remained at 33 °C in both summer experiments (Figs. 3a, 4a).

Whether the summer upper thermal limit for corals can be increased through short-term acclimatisation, and if so, by how much, remains to be investigated. The potential for thermal acclimation in corals was first shown by Coles and Jokiel (1978) who found that colonies of *Montipora verrucosa*, acclimatised for 56 days at 28 °C, experienced increased survivorship when exposed to 30 °C for three days and 32 °C for four days, compared to colonies incubated at 26 °C, 24 °C or

20 °C and then exposed to the same temperature treatments. Short-term thermal acclimatisation was also implicated in the recovery of corals downstream from a thermal effluent stream of a power plant following a natural bleaching event (Meesters and Bak 1993). Regeneration of experimentally induced lesions in bleached *Porites astreoides* in the thermal effluent stream was faster than bleached colonies outside the effluent stream. Similarly, *Echinopora gemmacea* undergoes seasonal acclimatisation in respiration and photosynthesis, although the pocilloporid, *Stylophora pistillata*, does not (Al-Sofyani and Davies 1992). A better understanding of the abilities of corals to acclimatise to thermal stress is needed to predict their likely fate during sea temperature anomalies.

In monitoring the recovery of experimentally heated corals, our results also show a substantial delay in the ultimate bleaching response of many colonies (Fig. 7). Overall, this delay was evident in the deterioration of nearly half the colonies in the first 34 days after thermal treatment, including colonies in apparently good health after the 5-day thermal stress period. This delay in response has important implications in the interpretation of natural coral bleaching events. Our results imply that factor(s) causing a natural bleaching event may be at critical levels a fortnight to a month prior to the onset of large-scale bleaching. Furthermore, field monitoring to determine the full extent of natural bleaching should be continued for a month or so after a stress event to document all colonies that may bleach or die.

The lack of difference in the thermal resistance of *P. damicornis* and *A. elseyi* between corals collected from the reef flat and slope (Fig. 4) was unexpected. Reef flat corals, which normally experience a highly variable temperature regime (up to 8 °C over 6 h), might be expected to have a higher upper thermal limit than their reef slope counterparts, which normally experience minimal diurnal variation (< 1 °C/day; Berkelmans and Oliver in preparation). The lack of habitat difference implies that daily, short-term variations in thermal history have limited potential to induce natural temperature acclimatisation in corals. In addition, reef slope corals would have experienced comparatively higher UV light in our experimental tanks than at their site of origin, whereas reef flat corals would have experienced approximately equivalent levels. The similar bleaching responses of reef slope and reef flat corals suggest that UV radiation levels were not high enough to cause a synergistic stress (e.g. Gleason and Wellington 1993) during these experiments. The lack of difference in the thermal resistance of *P. damicornis* colonies collected from Pelorus and Orpheus islands was also unexpected given the quite different responses of colonies from these two sites during the 1994 bleaching event. Factors other than temperature may have contributed to the differential in situ bleaching at these two sites.

In summary, our results highlight that upper thermal limits in coral populations at Orpheus Island, as in

other reef regions, are only slightly above ambient mean summer temperatures, although a small amount of seasonal variation in upper thermal limits can take place. Seasonal variation in upper thermal limits suggests that coral species may have some potential to acclimatise to elevated temperatures. For temperatures inducing moderate levels of stress, a substantial delay may exist before symptoms of bleaching become evident. Moreover, the severity of bleaching can continue to increase for at least four weeks after removal of the thermal stress. This delayed response must be taken into account in evaluating potential sources of stress in natural bleaching events.

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